Breeding Habitat Requirements and Colony Formation by Royal Terns (*Thalasseus Maximus*) and Sandwich Terns (*T. Sandvicensis*) on Barrier Islands in the Gulf of Mexico

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Source: The Auk, 129(4):763-772.
Published By: The American Ornithologists' Union
URL: http://www.bioone.org/doi/full/10.1525/auk.2012.11181

The Auk 129(4):763–772, 2012
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Printed in USA.

BREEDING HABITAT REQUIREMENTS AND COLONY FORMATION BY ROYAL TERNS (*THALASSEUS MAXIMUS*) AND SANDWICH TERNS (*T. SANDVICENSIS*) ON BARRIER ISLANDS IN THE GULF OF MEXICO

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Abstract.—Restoration and maintenance of barrier islands to preserve structural integrity and protect against erosional forces is a common goal of coastal protection. An assessment of restored barrier islands for their suitability as wildlife habitat is crucial for improvement of restoration methods and conservation of barrier-island-dwelling species, especially ground-nesting waterbirds. During the 2008 and 2009 breeding periods, we conducted a quantitative assessment of colonial waterbird use of the Isles Dernieres Barrier Island Refuge (IDBIR), Louisiana, which has experienced several restoration projects since the early 1990s, to understand the breeding ecology of two terns in the genus *Thalasseus* and investigated why some restored areas have not been colonized. Our objectives were to determine hatching success of the two species, identify important habitat characteristics for their reproduction and colony formation, and evaluate the success of past restoration efforts in providing suitable nesting habitat. Habitat characteristics were important for hatching success, including spatial attributes of nest sites and substrate composition. Discriminant function analysis revealed that suitable habitat for colony formation was available at some inactive restored areas, but the majority of inactive areas were unsuitable. The paucity of nesting activity at potentially suitable restored areas may be attributable to the greater activity of mammalian predators that we detected at inactive areas than at active colony sites. Management of restored barrier islands for specific waterbird habitat requirements, creation of new islands containing suitable ground-nesting habitat, and appropriate control of mammalian predators are critical factors for effective waterbird conservation and ecosystem function in these disturbance-prone regions. *Received 19 August 2011, accepted 21 May 2012.*

Key words: barrier islands, coastal restoration, ground-nesting waterbirds, Gulf of Mexico, habitat requirements, nest-site selection, *Thalasseus*.

Requerimientos del Hábitat Reproductivo y Formación de Colonias de *Thalasseus maximus* y *T. sandvicensis* en Islas Barrera en el Golfo de México

Resumen.—La restauración y el mantenimiento de las islas barrera para preservar la integridad estructural y brindar protección contra las fuerzas erosivas es una meta común de la protección costera. Una evaluación de la idoneidad de islas barrera restauradas como hábitats de vida silvestre es crucial para la mejora de los métodos de restauración y la conservación de especies que viven en las islas barrera, especialmente de aves acuáticas que anidan en el suelo. Durante los periodos reproductivos de 2008 y 2009, realizamos una evaluación cuantitativa del uso por parte de aves acuáticas coloniales de las islas del Dernieres Barrier Island Refuge (IDBIR), Louisiana, las cuales han experimentado varios proyectos de restauración desde principios de la década de 1990. Buscamos entender la ecología reproductiva de dos gaviotines del género *Thalasseus* e investigar por qué algunas de las áreas restauradas no han sido colonizadas. Nuestros objetivos fueron determinar el éxito de eclosión de las dos especies, identificar características importantes del hábitat para su reproducción y la formación de colonias, y evaluar el éxito de los esfuerzos de restauración pasados en proveer un hábitat de anidación adecuado. Las características de hábitat fueron importantes para el éxito de eclosión, incluyendo atributos espaciales de los sitios de anidación y la composición del sustrato. Un análisis de función discriminante reveló que el hábitat adecuado para la formación de colonias estaba disponible en algunas áreas restauradas pero inactivas, pero que la mayoría de las áreas inactivas no eran adecuadas para este fin. La falta de actividad de anidación en áreas restauradas potencialmente adecuadas puede ser atribuido a una mayor actividad de mamíferos depredadores detectada en áreas inactivas con respecto a sitios de colonias

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The Auk, Vol. 129, Number 4, pages 763–772. ISSN 0004-8038, electronic ISSN 1938-4254. DOI: 10.1525/auk.2012.11181

activas. La administración de las islas barrera restauradas para cumplir los requerimientos de hábitat específicos de aves acuáticas, la creación de nuevas islas que contengan hábitat adecuado para la anidación en tierra y un control apropiado de los mamíferos depredadores son factores críticos en la conservación efectiva de aves acuáticas y el buen funcionamiento de los ecosistemas en estas regiones propensas al disturbio.

Barrier islands have received considerable attention because of their critical function in hurricane protection (Martinez et al. 2009) and marsh erosion control (Stone and McBride 1998). Currently, the Louisiana coast is eroding at rates up to 100 km^2 year^{-1} and the state's barrier islands are eroding at ~8.2 m year^{-1} (Martinez et al. 2009). Loss of these islands would have dramatic effects on coastal ecosystems and species dependent on them. Rapid degradation of barrier islands is facilitated by wind and wave erosion, diminished sand supply coupled with subsidence, and relative sea-level rise (Dingler et al. 1993). Wave energy from hurricanes accounts for 90% of the shoreline retreat in Louisiana during the past century (Stone et al. 1997), while subsidence and reduced accretion make these areas more vulnerable to erosive forces (Barras et al. 2003).

Louisiana's barrier islands provide critical breeding grounds for numerous organisms, especially colonial waterbirds. Colonial ground-nesting waterbirds are dependent on barrier islands and are directly affected by island degradation. For example, Louisiana populations of the Sandwich Tern (*Thalasseus sandvicensis*) and Royal Tern (*T. maximus*) historically accounted for 77% and 16%, respectively, of the U.S. breeding populations (Spendelow and Patton 1988). Because Royal and Sandwich terns rely on sandy, remote, quadruped-free sites for nesting, Shealer (1999) and Buckley and Buckley (2002) identified erosion and development of barrier islands and insufficient maintenance of dredge-spoil islands as their primary conservation threats. Additionally, 11 waterbird species of conservation concern in Louisiana use barrier islands for nesting, resting, and wintering areas (Louisiana Department of Wildlife and Fisheries [LDWF] 2008). The Isles Dernieres Barrier Island Refuge (IDBIR) is particularly important to breeding waterbirds because they sustain some of the largest remaining breeding colonies in Louisiana (Michot et al. 2003). Erosion models have estimated that the island chain may become submerged before 2020 (Penland et al. 1988).

Rapid habitat loss has forced waterbird populations to rely more heavily on created and restored habitats (Parnell et al. 1997, Erwin et al. 2003). As colonial waterbirds experience increased pressures from human population growth and development, management and restoration of barrier islands has become a high priority for waterbird conservation. However, little work has been undertaken to evaluate the success of restoration in providing ecosystem functions, such as maintaining suitable habitat for ground-nesting waterbirds. Royal and Sandwich tern breeding habitat has been described only in the mid-Atlantic United States (Buckley and Buckley 1972, Blus et al. 1979) and Patagonia, Argentina (Quintana and Yorio 1997). The few quantitative assessments of breeding waterbirds' utilization of restoration sites that have been performed have demonstrated mixed results. Some restored areas have been detrimental to waterbird populations (e.g., Erwin and Beck 2007), whereas others have been beneficial, especially when mammalian predators are absent (Erwin et al. 2003, McGowan et al. 2005).

Restoration efforts at IDBIR have delayed its submergence and provided significant amounts of dune and beach habitat. Unfortunately, the majority of restored habitat on the IDBIR is not used by nesting waterbirds, despite apparent suitability for nesting and close proximity to foraging areas (M. Carloss, LDWF, pers. comm.). Advancing our understanding of waterbird breeding-habitat requirements is essential to improve management and restoration efforts focused on ecosystem sustainability of barrier islands. This information is also of paramount importance to waterbird conservation in the northern Gulf of Mexico, especially as habitat degradation continues and historically large waterbird colonies decline (Michot et al. 2003, Hunter et al. 2006).

Reproductive performance has been identified as a critical indicator of breeding-habitat quality (Franklin et al. 2000) but has not been applied extensively to waterbirds breeding on barrier islands. Differences in habitat characteristics such as substrate, vegetation, and elevation may influence waterbird use and reproductive success of restored habitats (Burger and Gochfeld 1990a, Nordstrom 2005, García-Borboroglu and Yorio 2007). Lack of colony formation and poor nesting success can also result from mammalian predation. Burger and Gochfeld (1990a) identified nine species of mammalian predators associated with Black Skimmer (*Rynchops niger*) colonies that affected breeding performance. Range expansion of mammalian predators on barrier island chains has been shown to reduce use by nesting waterbirds (Erwin et al. 2001).

Our objectives were to determine hatching success of two ground-nesting tern species, identify critical nest-site characteristics that influence hatching success, and evaluate the success of past restoration efforts in providing suitable habitat for colony formation at the IDBIR. We quantified the habitat requirements for both species and nesting habitat availability on restored, inactive sites and restored, active colony sites. Additionally, we determined differences in mammalian predator activity between restored, inactive sites and active colony sites.

Methods

Study area and focal species.—The present study was conducted in the Gulf Coast Prairies and Marshes Ecoregion of the Terrebonne Basin, at the IDBIR, Louisiana (Fig. 1). The refuge includes Raccoon, Whiskey, Trinity, and Wine islands, which encompass ~33 km of barrier islands located 13 km south of Cocodrie, Louisiana. All four islands have experienced dredge applications and vegetative plantings to create dune habitat (Louisiana Office of Coastal Protection and Restoration 2010). In addition, Raccoon and Wine islands have been protected by rock breakwater structures. Raccoon Island was bisected by Hurricane Andrew in 1992; therefore, we refer to East Raccoon Island, which is protected by rock structures, and West Raccoon Island, unprotected by rock structures, as separate study sites.

Royal and Sandwich terns were selected as focal species because they are ground-nesting waterbirds that nest on upper beach

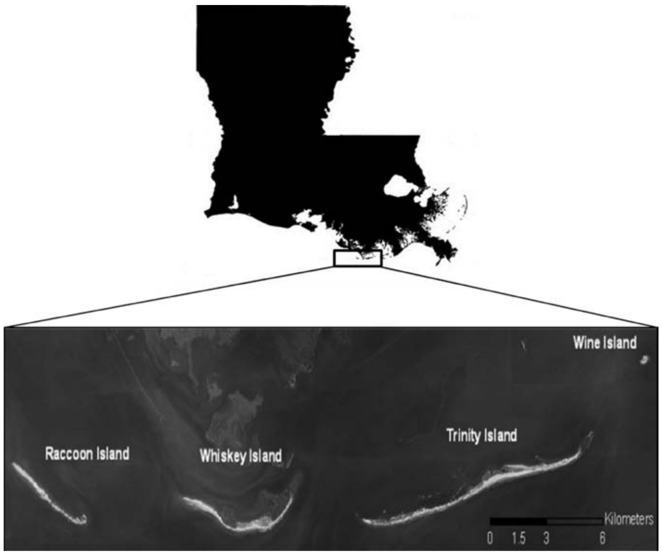

Fig. 1. The Isles Dernieres barrier islands and their location in Louisiana.

and dune habitats, which have been the focus of restoration efforts on the IDBIR. Royal and Sandwich terns are piscivorous, colonial waterbirds that nest in dense, mixed-species colonies on coastal habitats in the southern United States (Shealer 1999, Buckley and Buckley 2002). Observations by IDBIR managers and aerial survey data (Michot et al. 2003) indicated large populations of breeding *Thalasseus* species on Raccoon and Wine islands, which provided appropriate sample sizes for study and held potential for establishing new colonies on currently inactive sites. Furthermore, only anecdotal evidence was previously available on nest-site characteristics important to reproductive performance of *Thalasseus* (Buckley and Buckley 1972).

Nest monitoring.—We conducted nest-monitoring surveys at all breeding colonies from April through July in 2008 and 2009. Colony sites were defined as the total nesting area occupied by ≥6 breeding pairs that were ≥100 m apart from the nearest colony and separated by unused substrate (Thompson and Slack 1982). After breeding colonies were identified, a random sample of nests was selected for weekly nest monitoring to estimate hatching success. We used a grid system with 5 × 5 m quadrats covering each colony to determine population size and randomly selected 3 to 5 nests of each species to monitor within each quadrat. The total number of nests monitored at each colony varied in proportion to the total number of nests in each colony (range: 12–179 monitored nests). Monitored nests were marked with a numbered tongue depressor in areas of hard substrate (grass or shell-dominated sand) or a 0.3-m wooden stake in areas of soft substrate (loose sand).

All nests were monitored weekly until chicks left the nest or the nest failed. Any nest that failed before the expected hatch date was examined for evidence of predation (avian or mammalian tracks or sign, broken eggshells, or punctured eggs) and flooding (colony over-wash or island erosion). Eggs were considered abandoned if they were cold after the second check or if adults were not seen in the area. Nests that contained abandoned eggs were recorded as unknown failures. Empty nests were considered successful if we could confirm that either nearby adults were with young of proper age or clean eggshell caps with loose and clean membranes were in or near the nest (Mabee 1997).

Nest-site habitat characteristics.—At each colony, a minimum of 30 monitored nests of Royal and Sandwich terns were randomly selected to measure habitat characteristics. After hatching, we measured nest-habitat characteristics using 0.25-m^2 circular plots centered on the nests. We collected substrate to a depth of ~3 cm within each plot to determine particle size. Sediment samples were returned to the laboratory, and a 450-g sample was measured and sieved using a series of U.S. standard testing sieves, including 4-mm, 2-mm, 500-μm, 250-μm, 125-μm, and 63-μm mesh sizes. The six-sieve set was manually shaken for 2 min, and particles collected in each sieve were then weighed to determine the percent weight of each size class. The substrate classes were then divided into four categories: (1) >2 mm, (2) 2 mm to >250 μm, (3) 250 μm to >63 μm, and (4) ≤63 μm.

Plant species in the 0.25-m^2 plots were identified, and average height was measured. Vegetation cover was measured by estimating the percent ground surface covered by each plant species in the plot. Distance to the nearest vegetation from the sampling-plot perimeter was also measured, classified as woody or herbaceous, and average height recorded. Distance to the nearest nest was measured from the center of sampling plots to the center of the nearest neighboring nest. Distance from the sampling plots to the nearest colony perimeter, nearest Laughing Gull (*Leucophaeus atricilla)* nest, high-tide line, and loafing area (i.e., area between high-tide line and colony perimeter used by resting *Thalasseus* spp.) was also recorded. Benchmarks were established near each colony by taking elevations of waypoints using a Thales Z-Max GPS receiver with a Thales antenna and RTK adaptor. Actual nest elevations were then measured within ±0.061 m using an automatic level and leveling rod.

Colony-formation habitat characteristics.—Potentially important habitat characteristics for colony formation were measured at active colonies (n = 12) on East Raccoon, West Raccoon, and Wine islands and at inactive sites (n = 24) on Trinity and Whiskey islands. Inactive sites were selected at restored sites that appeared to be appropriate habitat for Royal and Sandwich tern colonies by at least two observers. Unfortunately, there were no unrestored control sites available for comparison to restored, active and restored, inactive sites. All variables measured at 0.25 m^2-plots during nest habitat sampling were averaged to provide mean values for each active site. At each inactive site, nine to thirty-two 0.25 m^2-plots were placed equidistantly throughout the inactive site. The number of sampling plots varied depending on the size of the area at each inactive site.

Additional colony-formation variables were also measured at active and inactive sites to characterize the habitat. Slope of sites was calculated by dividing the difference of high-tide elevation from mean site elevation by the distance to the high-tide line. We measured distance to high-tide line from the center of each site and distance to the nearest vegetated area from the perimeter of each site using a measuring tape, and distance to nearest active colony using ARCVIEW, version 9.3 (ESRI, Redlands, California). High-tide elevation in relation to each colony and the center colony elevation was measured using surveying equipment described previously. We estimated the percentage of ground surface covered by vegetation and the percentages covered by woody and herbaceous vegetation, and we measured the average height of vegetation along the perimeter at each site.

Mammalian predator activity.—We conducted scent-station track surveys to quantify mammalian predator activity on all islands (Roughton and Sweeny 1982, Sargeant et al. 2003). Mammalian predator surveys were conducted monthly in June and July 2008 and from April through July 2009. In 2008, we established 21 transects: 1 transect on Wine Island, 9 transects on Trinity Island, 5 transects on Whiskey Island, 2 transects on East Raccoon Island, and 4 transects on West Raccoon Island. The same transects were used in 2009 except for East Raccoon Island, where two additional transects were placed, and only one transect on West Raccoon Island was used because of land loss.

Each transect consisted of five scent stations, spaced 50 m apart, and transects were ≥400 m apart along the islands' beachfront. All scent stations were placed >50 m from active colonies to minimize risk of predation. We conducted surveys during periods of no precipitation and minimal winds. At each station, we traced a 1-m-diameter circle in the ground, covered it with sifted sand and mineral oil to create a suitable tracking surface, and placed a fatty-acid scent tablet in the center of the plot. We checked transects within 3 h of sunrise the following day, and recorded any mammalian predator activity (tracks) left inside the stations. A mammalian predator visit was defined as the presence of one or more mammalian predator tracks in the scent station.

Statistical analyses.—We estimated hatching success using the apparent method for ground nests on islands (i.e., number of nests to hatch at least one egg divided by total number of nests monitored; Johnson and Shaffer 1990). We used analysis of variance (ANOVA), and Kruskal-Wallis tests when the assumption of normality was not met, with Tukey-Kramer multiple comparison tests ($\alpha = 0.05$) to determine whether mean colony nest success differed between years and among islands (Sokal and Rohlf 1995, SAS Institute 2009).

We used Akaike's information criterion corrected for small samples sizes (AIC_c; Burnham and Anderson 2002) to determine important habitat characteristics for hatching success of Royal and Sandwich terns (successful = 1, failed = 0). Habitat variables included in the modeling were distance to colony perimeter, distance to high-tide line, distance to loafing area, distance to nearest nest, distance to nearest Laughing Gull nest, distance to nearest vegetation, percent vegetation cover, vegetation species richness, average vegetation height, average height of nearest vegetation, nest elevation, percent debris cover, substrate color, and four substrate size classes. Competing models were constructed from the measured variables, but only models with a ΔAIC_c value within 2 AIC_c of the top model were retained. We used Pearson correlation to evaluate correlations among all parameters included in the candidate models and found low correlation among parameters (all $r < 0.7$). Parameter likelihoods of each habitat variable were calculated by summing the AIC_c weights of all models containing those variables. We calculated model-averaged estimates for coefficients and standard error terms for each parameter from all candidate models based on model AIC_c weights (Burnham and Anderson 2002). Important habitat characteristics (parameter likelihood > 0.50) were then examined with univariate analysis between successful and failed nests. All statistical analyses were conducted in SAS, version 9.2 (SAS Institute, Cary, North Carolina).

We used 11 habitat variables to model colony formation in Royal and Sandwich terns: mammalian predator activity index, percent woody cover along site perimeter, percent herbaceous cover along site perimeter, percent vegetated cover at site, mean elevation, slope, difference between site elevation and high-tide-line elevation, shortest distance to high-tide line, high-tide elevation, distance to nearest colony, and distance to nearest vegetated area. Factor analysis (FA) was performed to establish a subset of uncorrelated variables that explained the relationships among the 11 original variables. A linear discriminant function analysis (DFA) model was then developed using jackknife procedures as cross-validation, based on the factor scores from the FA results, to predict the classification of the 36 study sites as active (12 sites) or inactive (24 sites).

We calculated an index of mammalian predator activity for each island by dividing the total number of mammalian predator visits by the total number of station-nights and multiplying by 1,000. Kruskal-Wallis ANOVA and Tukey-Kramer multiple comparison tests were used to determine whether differences existed in mean activity indices between years and site types ($\alpha = 0.05$). Statistics are reported as means ± SE.

Results

Descriptive statistics.—In both years, the IDBIR supported substantial numbers of breeding pairs of Royal (range: 490–6,900; Table 1) and Sandwich terns (range: 340–4,240; Table 1). The mean colony nest initiation date of Royal Terns in 2008 (3 May ± 2.2 days) was earlier ($F = 6.07$, df = 1, $P = 0.048$, $n = 12$) than that in 2009 (13 May ± 4.3 days). There was no difference in mean colony initiation date among islands for Royal Terns or among year × island interactions. For Sandwich Terns ($n = 11$ colonies), there was no difference in mean colony initiation date among islands or between 2008 (10 May ± 2.7 days) and 2009 (18 May ± 2.3 days). The mean initiation date of Royal Tern nests (5 May ± 0.3 days) was earlier ($F = 187.8$, df = 1, $P < 0.01$, $n = 1{,}350$) than the mean initiation date of Sandwich Tern nests (11 May ± 0.3 days).

The mean clutch size of Royal Terns with nests pooled among years was 1.03 ± 0.01 ($n = 820$ nests; range: 1–2 eggs). Two-egg clutches of Royal Terns represented 4% of 417 nests in 2008 and 2% of 403 nests in 2009. Similarly, mean clutch size of Sandwich Terns with nests pooled among years was 1.07 ± 0.01 ($n = 530$ nests; range: 1–3 eggs). Two-egg clutches of Sandwich Terns represented 8% of 250 nests in 2008 and 6% of 280 nests in 2009; only one clutch of three eggs was found.

Mean distance to nearest nest pooled among years was 0.34 ± 0.01 m ($n = 302$) and 0.30 ± 0.002 m ($n = 237$) for Royal Terns and Sandwich Terns, respectively, and mean colony nearest-nest distance did not differ between years or among islands for either species.

Hatching success.—We monitored 500 Royal Tern nests among seven colonies in 2008 and 470 nests among five colonies in 2009 (Table 1). Mean island hatching success ranged from 69% to 93% over both years, with an overall mean of 82 ± 6.7% and 86 ± 3.5% in 2008 and 2009, respectively. Mean colony hatching success did not differ by year ($F = 0.09$, df = 1, $P = 0.7$, $n = 12$) or by island ($F = 0.44$, df = 2, $P = 0.6$, $n = 12$). Predation, flooding, and unknown causes of failure accounted for 40%, 26%, and 34%, respectively, of nest failure over both seasons. In both years, predation was the most important known cause of nest failure on East

TABLE 1. Total number of nests per island, number of monitored nests (n), hatching success, and percentage of nests affected by predation (P), flooding (F), or unknown failure (U) by species at the Isles Dernieres Barrier Islands Refuge, Louisiana, 2008 and 2009.

		2008						2009					
Species	Island	Total nests	n	Percent success	% P	% F	% U	Total nests	n	Percent success	% P	% F	% U
Royal Tern	East Raccoon	6,900	215	91	4.2	0.5	4.6	4,190	265	82	13.2	0.8	4.5
Royal Tern	West Raccoon	3,080	134	69	7.5	17.1	6.7	490	41	83	4.9	4.9	7.3
Royal Tern	Wine	3,140	151	86	2.6	2.6	8.6	2,830	164	93	0	4.3	3.0
Totals		13,120	500	82	4.6	5.6	6.4	7,510	470	86	7.8	2.3	4.3
Sandwich Tern	East Raccoon	400	36	93	2.8	0	2.7	2,530	151	78	7.3	2	9.2
Sandwich Tern	West Raccoon	4,240	137	71	9.5	2.9	2.9	340	33	82	3.0	0	15.2
Sandwich Tern	Wine	4,310	134	76	9.7	2.2	11.9	2,870	153	86	2.6	1.3	9.8
Totals		8,950	307	80	8.8	2.3	7.5	5,740	337	82	5.3	1.5	10.0

Raccoon, whereas flooding was the most important known cause of nest failure on West Raccoon in 2008 and on Wine in 2009 (Fig. 2A). Predation and flooding were equally important known causes of nest failure on Wine in 2008 and on West Raccoon in 2009.

A total of 307 Sandwich Tern nests among six colonies in 2008 and 337 nests among five colonies in 2009 were monitored (Table 1). Mean island hatching success ranged from 71% to 93% over both years, with an overall mean of 80 ± 6.7% and 82 ± 2.3% in 2008 and 2009, respectively. Mean colony hatching success did not differ by year (F = 0.01, df = 1, P = 0.9, n = 11) or by island (F = 0.5, df = 2, P = 0.6, n = 11). Predation, flooding, and unknown causes of failure accounted for 39%, 11%, and 50%, respectively, of nest failure over both seasons. Predation was the leading known cause of nest failure on all islands and in both years (Fig. 2B).

Modeling hatching success.—Thirty-one habitat models were retained ($\Delta AIC_c < 2$) for Royal Tern hatching success and 41 habitat models were retained for Sandwich Tern hatching success. All models performed poorly, but Table 2 provides the top models for both Royal and Sandwich terns based on model weights ($w_i > 0.03$). Retained habitat models for Royal Tern hatching success included all 17 habitat variables, and Sandwich Tern models included all variables except nest elevation (Table 3). However, parameter likelihoods of variables (Table 3) identified several spatial attributes of nest sites and substrate composition to be important (parameter likelihood > 0.50) for both Royal and Sandwich tern hatching success.

Considering variables with parameter likelihoods >0.50 (Table 3), distance to colony perimeter was positively correlated with hatching success of both Royal and Sandwich terns, whereas distance to loafing area was negatively correlated with hatching success of both species. Distance to high-tide line was also positively correlated with Royal Tern hatching success. Distances to nearest nest and nearest vegetation were negatively correlated with Sandwich Tern hatching success. Some substrate size classes also had high parameter likelihoods for both species (Table 3). Univariate analysis of important habitat variables (parameter likelihood > 0.50) supported habitat modeling, in that distance to colony perimeter and high-tide line were greater at successful Royal Tern nests than at failed nests (Table 4). For Sandwich Terns, distances to loafing area and nearest vegetation were less at successful than at failed nests (Table 4).

Colony-formation habitat suitability.—Factor analysis established a subset of uncorrelated variables that explained >97% of the variability among the 11 habitat variables (Table 5). Variables that were highly correlated with FA factors included percent herbaceous cover along site perimeter and percent vegetated cover at the site with factor 1; site elevation, difference between site and high-tide elevation with factor 2; and site elevation, high-tide elevation, difference between site and high-tide elevation, and

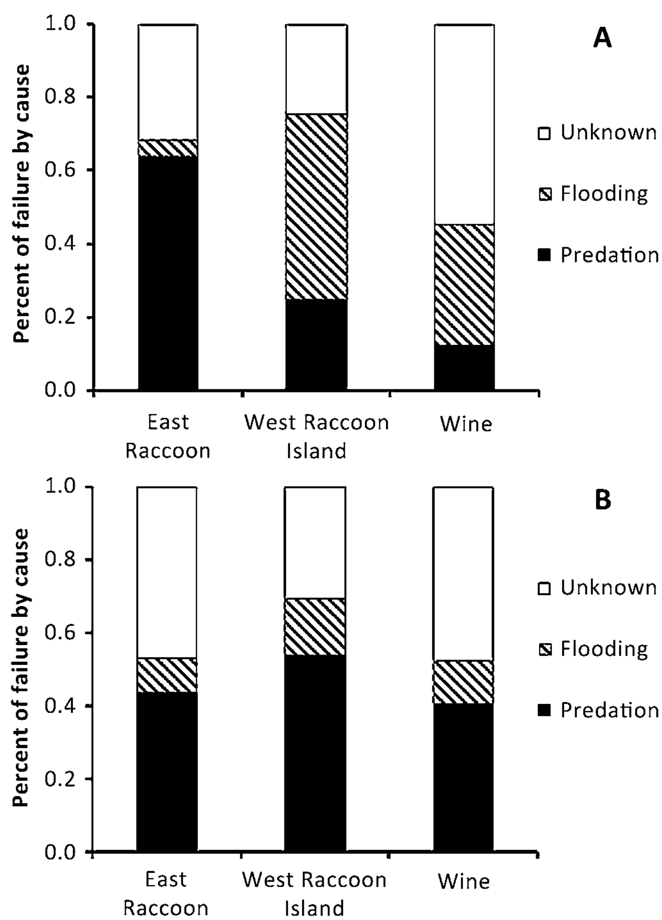

FIG. 2. Causes of nest failure for (A) Royal Terns and (B) Sandwich Terns on three breeding islands in the Isles Dernieres barrier islands, 2008–2009.

Table 2. Habitat models for hatching success of Royal Terns and Sandwich Terns at Isles Dernieres Barrier Island Refuge, Louisiana, 2008–2009, with number of parameters (k), difference in Akaike's information criterion adjusted for small sample size (ΔAIC_c) from top model ($AIC_c = -525.252$), and model weights (w_i). Models presented include only those with a $w_i > 0.03$.

Model	k	ΔAIC_c	w_i
Royal Tern hatching success			
VegSpp + DistHt + DistLoaf + DistColPer + Size2 + Size4	6	0	0.0663
DistHt + DistLoaf + DistColPer + Size1 + Size2 + Size3 + Size4	7	0.249	0.059
DistHt + DistLoaf + DistColPer + Size2 + Size4	5	0.508	0.051
VegSpp + DistHt + DistLoaf + DistColPer + Size1 + Size2 + Size3 + Size4	8	0.725	0.046
VegHt + DistHt + DistLoaf + DistColPer + Size2 + Size4	6	0.814	0.044
NearVeg + DistHt + DistLoaf + DistColPer + Size2 + Size4	6	1.004	0.0401
VegHt + DistHt + DistLoaf + DistColPer + Size1 + Size2 + Size3 + Size4	8	1.112	0.038
VegSpp + DistHt + DistColPer + Size2 + Size4	5	1.381	0.033
SubColor + DistHt + DistLoaf + DistColPer + Size2 + Size4	6	1.429	0.032
NearVeg + DistHt + DistLoaf + DistColPer + Size1 + Size2 + Size3 + Size4	8	1.470	0.032
VegSpp + DistHt + DistLoaf + DistColPer + DistGullNest + Size2 + Size4	7	1.514	0.031
Sandwich Tern hatching success			
NearVeg + DistLoaf + NearNest + DistColPer + Size4	5	0	0.046
NearVeg + DistLoaf + NearNest + Size4	4	0.244	0.041
NearVeg + DistHT + DistLoaf + NearNest + DistColPer	5	0.280	0.040
NearVeg + DistLoaf + NearNest + DistColPer	4	0.524	0.035
NearVeg + DistHT + DistLoaf + NearNest	4	0.647	0.033

distance to nearest vegetated area with factor 3. The DFA model included all three factors from FA and was significant with Wilks's lambda ($P < 0.001$). The DFA correctly classified 75% of the 36 study sites as active or inactive (Fig. 3). Five active sites and four inactive were classified incorrectly. All misclassifications occurred along the boundary between correctly classified active and inactive sites (Fig. 3). Inactive sites classified as active differed from active sites primarily along the factor 3 axis, representing higher elevations and sparser vegetation (Table 5). Active sites classified as inactive differed from inactive sites mainly along the factor 2 axis, correlated with lower differences between nests and high-tide elevations and greater vegetation cover (Table 5).

Mammalian predator activity.—Visits by Raccoons (*Procyon lotor*), rats (*Rattus* sp.), and Coyotes (*Canis latrans*) comprised 71%, 25%, and 4%, respectively, of the total scent-station visits in 2008 and 2009. The mean mammalian predator activity index did not differ between years ($\chi^2 = 0.2$, df = 1, $P = 0.65$, $n = 14$) but was greater at inactive sites ($n = 8$), with a mean of 158.0 ± 32.03, compared with an average of only 2.08 ± 37.09 ($n = 6$) at active sites ($\chi^2 = 9.6$, df = 1, $P = 0.001$).

Discussion

During our 2-year study, there were consistently high breeding populations and hatching success of Royal and Sandwich terns on the IDBIR, indicating that high-quality nesting habitat is available on these islands. Although comparative data on hatching success for both Royal and Sandwich terns are limited, hatching success on the IDBIR was comparable to or higher than previously reported from South Carolina (Blus et al. 1979), Patagonia (Quintana and Yorio 1997), and England (Langham 1974). Hatching success in IDBIR was less variable over our 2 years of study than during some previous studies; for example, hatching success

Table 3. Summary of parameter likelihood for hatching success of Royal and Sandwich terns at Isles Dernieres Barrier Island Refuge, Louisiana, 2008–2009, calculated by summing the AIC_c weights of all models containing those variables and model-averaged parameter estimates (SE) for all variables included in habitat models ($\Delta AIC_c < 2$).

	Royal Tern		Sandwich Tern	
Variable	Parameter likelihood	Estimate ± SE	Parameter likelihood	Estimate ± SE
Distance to colony perimeter	1.000	0.215 ± 0.087	0.533	0.075 ± 0.053
Distance to high tide line	1.000	0.034 ± 0.010	0.338	0.004 ± 0.003
Distance to loafing area	0.967	−0.020 ± 0.010	0.950	−0.020 ± 0.009
Distance to nearest nest	0.025	−0.022 ± 0.091	1.000	−9.822 ± 4.078
Distance to nearest gull nest	0.089	−0.005 ± 0.005	0.122	0.009 ± 0.008
Distance to nearest vegetation	0.099	−0.039 ± 0.045	1.000	−0.777 ± 0.248
Percent vegetation cover	0.074	0.0002 ± 0.0004	0.081	0.021 ± 0.007
Vegetation species richness	0.440	0.173 ± 0.124	0.080	0.017 ± 0.024
Vegetation height	0.110	0.165 ± 0.158	0.073	0.065 ± 0.107
Height of nearest vegetation	0.053	0.053 ± 0.055	0.056	0.028 ± 0.040
Nest elevation	0.025	−0.001 ± 0.011	NA	NA
Percent debris cover	0.025	−0.0004 ± 0.002	0.115	0.013 ± 0.015
Substrate color	0.087	0.021 ± 0.025	0.079	−0.025 ± 0.023
Substrate size class 1	0.387	−1.200 ± 0.612	0.064	−0.158 ± 0.068
Substrate size class 2	0.949	−1.222 ± 0.619	0.084	0.157 ± 0.068
Substrate size class 3	0.386	−1.191 ± 0.612	0.128	0.161 ± 0.070
Substrate size class 4	1.000	−4.256 ± 1.628	0.538	1.057 ± 0.629

Table 4. Comparisons of important habitat characteristics (parameter likelihood > 0.50) for Royal Tern (failed nests = 72 and successful nests = 230) and Sandwich Tern (failed nests = 66 and successful nests = 171) hatching success between failed and successful nests at Isles Dernieres Barrier Island Refuge, Louisiana, 2008–2009.

		Mean ± SE		
Species	Habitat variable	Failed nests	Successful nests	*t* (*P*)
Royal Tern	Distance to colony perimeter (m)	2.08 ± 0.21	2.66 ± 0.13	2.28 (0.01)
	Distance to high tide line (m)	29.68 ± 1.84	35.70 ± 1.44	2.17 (0.02)
	Distance to loafing area (m)	23.71 ± 1.75	22.09 ± 1.06	0.76 (0.45)
	Percent of substrate size class 2	71.32 ± 1.42	69.36 ± 0.82	1.17 (0.24)
	Percent of substrate size class 4	0.15 ± 0.02	0.15 ± 0.01	0.20 (0.84)
Sandwich Tern	Distance to colony perimeter (m)	2.53 ± 0.23	2.72 ± 0.13	0.73 (0.47)
	Distance to loafing area (m)	25.70 ± 1.92	20.40 ± 1.25	2.26 (0.02)
	Distance to nearest nest (m)	0.30 ± 0.01	0.29 ± 0.001	1.64 (0.10)
	Distance to nearest vegetation (m)	0.55 ± 0.10	0.26 ± 0.04	3.21 (0.001)
	Percent of substrate size class 4	0.15 ± 0.01	0.19 ± 0.02	1.29 (0.19)

of Sandwich Terns (*T. s. sandvicensis*) in England varied from 54% to 96% over a 3-year period (Langham 1974).

Primary causes of nest failure varied among islands. Flooding was an important cause of nest failure on West Raccoon and Wine islands, especially for peripheral nests that were adjacent to unprotected and eroding shorelines. The presence of rock breakwaters along East Raccoon Island's shoreline may have diminished the effect of erosion on tern colonies and protected nests from flooding, which has been suggested previously by Broussard and Boustany (2005). Egg predation by avian predators may be an important source of nest failure. Although rates of avian nest predation were not quantified, Laughing Gulls were observed depredating nests on East Raccoon Island and may account for some of the unknown nest failures. Avian predators have been shown to have a significant negative effect on hatching success through both direct and indirect effects of predation (Nisbet and Welton 1984).

Overall, habitat models performed poorly in explaining the variation in hatching success. High hatching success of both species, which probably resulted from (1) the high-quality nesting habitat found at the sites combined with (2) the fairly random nature of nest failure, resulted in many generally equivalent models. In addition, there is considerable homogeneity among beach nesting habitats, which may limit the ability of habitat variables to explain difference in hatching success. The chance occurrence of opportunistic nest predation most likely drove the majority of variation in hatching success, although, as observed in other waterbird species (Bollinger 1994), differences in parental quality may also have contributed.

Habitat modeling of Royal and Sandwich terns' hatching success identified several variables (based on parameter likelihoods; Table 3) related to spatial attributes of nests and substrate composition that may be important for successful nesting. Royal and Sandwich terns' hatching success was influenced by nest placement in relation to sources of nest failure: nest predators or inundation. Greater distances of nests to colony perimeter may provide protection for nests from predators. Nest predators, including Laughing Gulls and Kelp Gulls (*Larus dominicanus*), specifically

Table 5. Factor loadings for habitat variables at active and inactive sites of Royal and Sandwich terns at Isles Dernieres Barrier Island Refuge, Louisiana, 2008–2009.

Habitat variable	Factor 1	Factor 2	Factor 3
Site predator activity index	–0.29	0.41	–0.15
Perimeter woody vegetation cover	0.24	–0.40	0.03
Perimeter herbaceous cover	0.61[a]	0.45*	–0.01
Site vegetation cover	0.73[a]	–0.26	0.12
Site elevation	–0.11	0.54[a]	0.49[a]
Slope	0.47	0.12	0.22
Difference between site and high-tide elevation	–0.19	–0.45[a]	0.40[a]
Nearest distance to high-tide line	–0.20	0.01	0.33
High-tide-line elevation	–0.40	0.07	0.49[a]
Nearest colony	–0.01	0.30	–0.35
Distance to nearest vegetated area	–0.41	–0.19	–0.40[a]

[a]Habitat variables most correlated with factor.

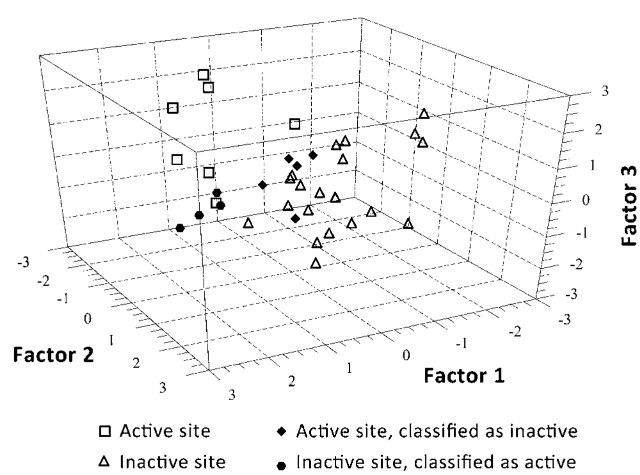

Fig. 3. Separation of correctly and incorrectly classified used and unused colonies in three-dimensional space defined by the first three axes from the linear discriminant function analysis of colony formation variables for Royal Terns and Sandwich Terns from the Isles Dernieres barrier islands, 2008–2009.

prey on nests located outside the colony center, where defensive mobbing may be less intense (Buckley and Buckley 1972, Yorio and Quintana 1997). Furthermore, greater distances between nest sites and high-tide lines may provide protection for nests from flooding, as Burger and Gochfeld (1990b) suggested for Least Tern nests.

Avian reproductive performance may be enhanced when energetic costs are reduced (Bryant 1988), and our results indicate that Sandwich and Royal terns benefited, in terms of hatching success, from nesting closer to loafing areas. Nesting close to a loafing area may contribute to breeding performance because easy access to a loafing area may reduce energy expenditures of breeding terns and enhance nest vigilance. Successful Sandwich Tern nests were closer to vegetation than failed nests. Nearby vegetation may provide protection against inclement weather and reduce exposure to flooding and erosion. Nesting in close proximity to vegetation has also been shown to benefit the reproductive performance of other colonial waterbirds (Burger and Lesser 1978, García-Borboroglu and Yorio 2007). Nesting near neighbors also tended to increase the probability of Sandwich Tern hatching success, which may be because having neighbors nearby helped reduce the probability of nest predation. Nesting in close proximity is a common trait of ground-nesting colonial waterbirds and may reduce the risk of predation (Wittenberger and Hunt 1985).

The hatching-success models also indicated that substrate was associated with hatching success of both tern species, but the reason(s) are not entirely clear. Preferences in substrate composition of ground-nesting waterbird habitat are poorly understood but have been found in Least Terns (*Sternula antillarum*; Thompson and Slack 1982), Caspian Terns (*Hydroprogne caspia*; Quinn and Sirdevan 1998), and Gull-billed Terns (*Gelochelidon nilotica*; Mallach and Leberg 1999).

Colonial waterbirds establish colonies in habitats that offer essential characteristics for their survival and reproduction (Lack 1968). Availability of nesting habitat and food, protection from predators, and social stimuli characterize suitable breeding sites (Buckley and Buckley 1980). Results of our multivariate analysis indicated that important habitat characteristics for colony formation included vegetative cover, site elevation, and distance to vegetated areas. Vegetation cover has been shown to influence the thermal properties of nesting areas and the risk of predation for waterbirds (Jehl and Mahoney 1987). Sparse to moderate herbaceous cover has also been shown to be an important characteristic for waterbird colony formation (Greer et al. 1988), although thick vegetation cover may also deter colonization (Soots and Parnell 1975). Vegetation may stabilize substrate and thereby reduce erosion of nests and provide protection for juvenile waterbirds from weather and predators. For example, Common Terns initiate colonies at sites with dense grass clumps (Kharitonov and Siegel-Causey 1988). Moreover, proximity to vegetated areas, which are usually located away from the ocean, may aid colonies in avoiding tidal flooding (Burger and Gochfeld 1990a).

Elevational features that were important for colony formation included mean elevation, high-tide elevation, and the difference between mean elevation and high-tide elevation. These elevational features reduce the probability of flooding, which is a major threat to colonial waterbirds in Louisiana (Greer et al. 1988). Elevation is of the utmost importance in colony site selection in other species of colonial waterbirds along the Atlantic coast (Burger and Gochfeld 1990b, Rounds et al. 2004).

Suitable habitat for colony formation was seemingly available at four restored yet inactive areas on the refuge (Fig. 3). The failure of breeding waterbirds to use these areas may be attributable to the greater activity of mammalian predators that we detected at these sites compared with active colonies. The use of habitat (five active sites) predicted to be inactive through our DFA suggests that *Thalasseus* species may select marginal habitats because of the absence of mammalian predators at these sites and the lack of available predator-free, high-quality nesting habitats. Failure to address predator activity has compromised other restoration projects that attempt to provide suitable nesting habitat for waterbirds (Erwin and Beck 2007, Erwin et al. 2011).

Without the intensive restoration efforts undertaken on Raccoon and Wine islands, these important colony sites would not exist to serve as nesting habitat for colonial waterbirds that require remote, disturbance-free islands. The consistently high reproductive performance of Royal and Sandwich terns at the IDBIR emphasizes the quality of this habitat and the need to restore and appropriately manage high-quality colony sites. The important habitat characteristics that we found to influence reproductive success and colony formation may be used to develop management plans for creating or restoring ground-nesting waterbird habitat within this region. Although the main goal of barrier-island restoration projects continues to be coastal protection, incorporating species' habitat needs may enhance the ecosystem function of these projects. Restoration projects that incorporate use of dredge material should consider potential colony site elevations and high-tide elevations to inhibit flooding, management for sparse to moderate vegetation cover, proximity to suitable loafing areas, and high-tide line. Rock breakwater structures, such as those on East Raccoon Island, also seemed to be important in protecting these high-quality colony sites from erosion and flooding. Breakwater structures may also minimize the need for periodic replenishment of dredge material on barrier islands; however, they may also accelerate erosion in some areas.

Our results show that some restored, inactive sites are suitable nesting habitats but that mammalian predator activity may inhibit breeding waterbirds from utilizing these sites. Removing mammalian predators is an effective conservation strategy for enhancing bird populations (Nordstrom et al. 2003, Smith et al. 2010). By quantifying habitat requirements for reproductive success, habitat suitability for colony formation, and mammalian predator activity on this refuge, we identified potentially important factors for evidence-based conservation (Sutherland et al. 2004) of ground-nesting waterbirds. Incorporation of these important factors into future restoration projects and their evaluation through adaptive management may dramatically improve their success (Erwin and Beck 2007, Erwin et al. 2011). Evaluating other fitness parameters such as fledging success and postfledging survival will also improve our understanding of waterbird responses to restoration. Improving our restoration capabilities is of paramount importance, considering the frequency of natural and anthropogenic disturbances that affect these critical breeding grounds, which has been emphasized, most recently, by the *Deepwater Horizon* oil spill. As waterbird breeding habitat continues to vanish in this region, informed management of remote barrier islands may be the only option for conserving coastal waterbird populations and ecosystem function and services, while simultaneously providing erosion control and storm protection.

Acknowledgments

This project was funded by a State Wildlife Grant from the Louisiana Department of Wildlife and Fisheries and the U.S. Fish and Wildlife Service (grant no. 940-40-4119). We thank our field assistants, B. Boudreaux, J. Bosler, T. Owen, K. Percy, and S. Youngren. Louisiana Universities Marine Consortium, Nicholls State University, and Louisiana State University provided valuable logistical support and equipment. G. Hepp and two anonymous reviewers provided helpful comments on the manuscript.

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Associate Editor: G. R. Hepp